

OCCURRENCE OF THE BIVALVE GENUS *MANTICULA* IN THE EARLY CRETACEOUS OF ANTARCTICA

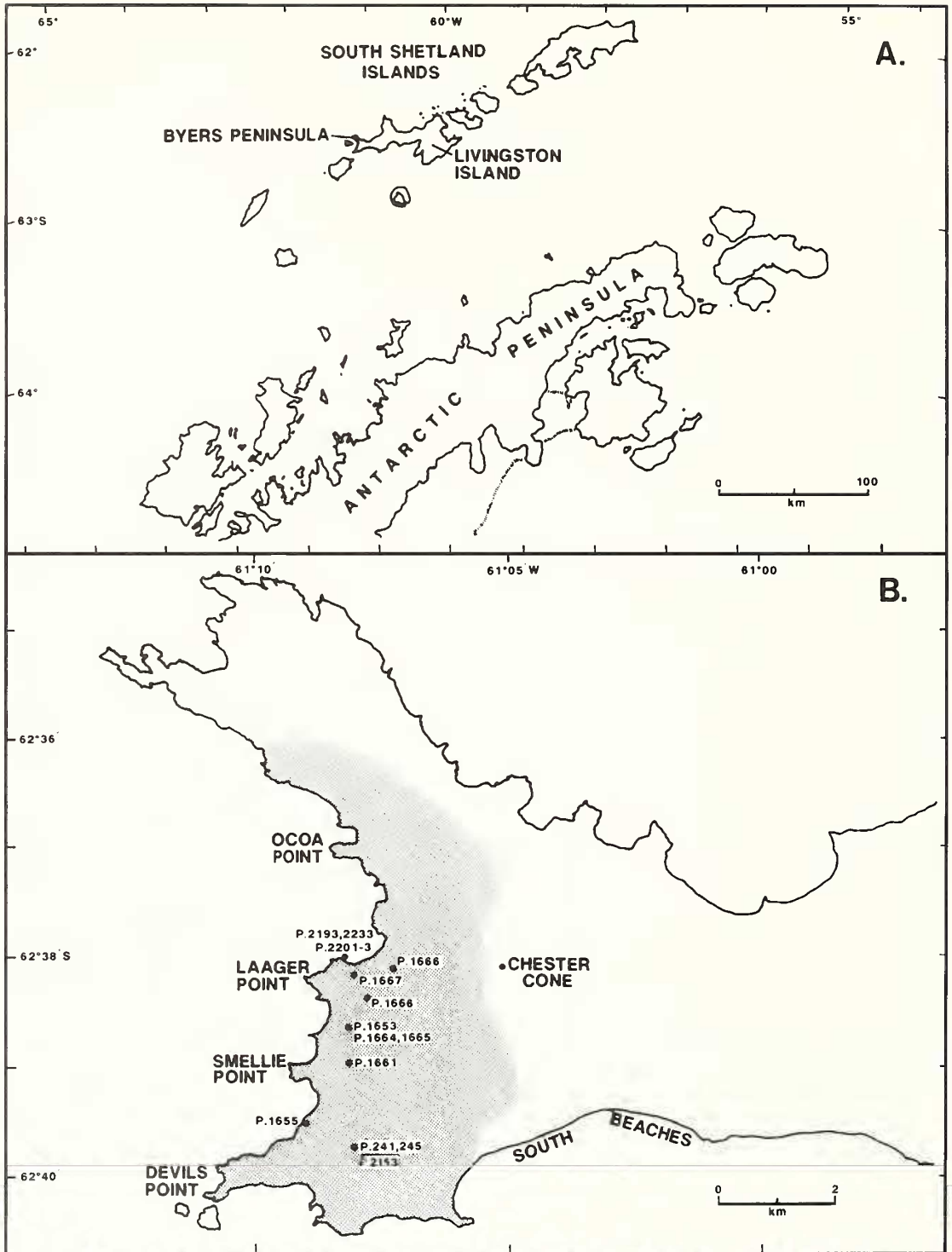
by J. A. CRAME

ABSTRACT. A new occurrence of a pergamidiid bivalve genus, which can probably be assigned to *Manticula* Waterhouse, 1960, is established within the Early Cretaceous (Berriasian) of Antarctica. Such a record is of particular interest as this taxon was only known previously from the Late Triassic of New Zealand and New Caledonia. The Antarctic material is contained within a new species, *M. complanata*, which is shown to be somewhat smaller and less inflated than the genotypic *M. problematica* (Zittel). There are indications from the Antarctic species that, at least in juvenile specimens, the hinge region of the left valve is characterized by a prominent saddle-shaped fold (or tooth) and a triangular resilifer. Using features such as these and details of the shell structure, it is possible to establish close links between *Manticula* and the pergamidiid genus *Krumbeckiella* on the one hand, and the eurydesmid genus *Eurydesma* on the other. The eurydesmid-pergamidiid group is essentially a Southern Hemisphere one with high-latitude origins in the Early Permian. Following a phase of expansion through the Triassic, it would appear to have retracted to the single Antarctic occurrence of *Manticula* in the Early Cretaceous.

DURING the course of systematic geological surveys, a thick sequence of Late Jurassic–Early Cretaceous marine clastic rocks was discovered on Byers Peninsula, western Livingston Island, South Shetland Islands (62° 38' S; 61° 04' W) (Smellie *et al.* 1980, 1984) (Text-fig. 1). This sequence is in places highly fossiliferous, and a variety of ammonite and belemnite types has been used to establish an age-range of at least Kimmeridgian–Valanginian (Smellie *et al.* 1980). Further field studies have recently been completed and an estimated 1 km thickness of mudstone-dominated lithologies has been combined into the new Byers Group. It is envisaged that these sediments accumulated in a marginal fore-arc setting (Crame *et al.* 1993).

Bivalves form a prominent component of the marine invertebrate macrofaunal assemblage from the lower levels of the Byers Group (principally the President Beaches Formation; Crame *et al.* 1993). Epifaunal types present include retroceramids, inoceramids, various oxytomids, occasional entoliids and several types of oyster; infaunal and semi-infaunal groups include nuculids, nuculanids, grammatodontids, trigoniids, astartids and other small heterodonts. An initial study (Crame 1984) identified a number of distinctive elements within this bivalve fauna, with perhaps the most unusual one being a small-medium, mytiliform and almost smooth taxon with superficial similarities to both the Buchiidae and Inoceramidae. Nevertheless, subsequent detailed examination revealed that it clearly could not be assigned to either of these families; it would seem, instead, to be referable to one of the lesser-known pteriomorph groups, the Pergamidiidae Cox, 1969.

The smooth, mytiliform Byers Peninsula taxon can probably be referred to the pergamidiid genus *Manticula* Waterhouse, 1960. Such a determination is of immediate biostratigraphical and biogeographical interest, for *Manticula* has hitherto been recorded from only the Late Triassic (Carnian–Norian) of New Zealand and New Caledonia; indeed, the stratigraphical range of the entire Pergamidiidae is only Upper Triassic–Lower Jurassic (Cox 1969). As the Byers Peninsula material is dated unequivocally as earliest Cretaceous (Berriasian; Crame *et al.* 1993), it would



TEXT-FIG. 1. Locality map for Byers Peninsula, western Livingston Island. A, The northern Antarctic Peninsula region. B, Byers Peninsula – showing localities at which *Manticula* has been collected and the outcrop of the lower part of the Byers Group (shaded). A more detailed geological map is given in Crame *et al.* (1993, fig. 1).

appear that *Manticula* might be a Lazarus Taxon (*sensu* Jablonski 1986), with no known Jurassic representative, and Antarctica serving as a last refuge for this formerly more widespread family.

SYSTEMATIC PALAEOONTOLOGY

Order PTERIOIDA Newell, 1965
 Suborder PTERIINA Newell, 1965
 Superfamily AMBONYCHIOIDEA Miller, 1877?
 Family PERGAMIDIIDAE Cox, 1969
 Genus MANTICULA Waterhouse, 1960

Type species. *Mytilus problematicus* Zittel (1864); by original designation.

Diagnosis. Small–medium (and occasionally large) mytiliform bivalves; prominent, pointed beaks; generally smooth but can exhibit low concentric folds and fine radial striae; largest forms may develop bizarre gibbous shape in ?RV; thickened, striated hinge region bears oblique, ridge-like fold or ‘tooth’ – this feature may become overthickened and obscured in large specimens; thickened shell largely calcitic – predominantly crossed-foliated?

Storage of Material: All Antarctic specimens (prefixed by P.) are housed in the collections of the British Antarctic Survey, Cambridge, UK. New Zealand specimens from the C. T. Trechmann Collection are housed in the Department of Palaeontology, Natural History Museum, London (NHM); specimens prefixed TM are located in the reference collections of the Institute of Geological and Nuclear Sciences, Lower Hutt, New Zealand.

Manticula complanata sp. nov.

Plate 1, figures 1–10; Plate 2, figures 1–2; Text-figure 2

Type material. Holotype: P. 241.9 (internal mould LV). Paratypes: P. 241.8, 10, 18, P. 245.10–12, P. 1667.1, 6–9, 11–18, 20, 21, 23–25, P. 1653.3, 4, P. 1655.9–11, P. 1661.16, P. 1664.21, P. 1665.8, 9, 12, 14, 15, P. 1666.1–4, P. 1668.3–10, P. 2193.83–85, 90–95, P. 2201.6, 7, 9, 11, 13–15, 17, 18, 20–22, P. 2202.19, P. 2203.1, P. 2153.80–82, P. 2233.4–12, 16, 17, 19. All the specimens were obtained from the President Beaches Formation, the principal lithostratigraphical unit within the lower Byers Group, western Byers Peninsula (Text-fig. 1).

Occurrence. As for the type material. Associated macrofossils date the President Beaches Formation as Berriasian (Smellie *et al.* 1980), and there are some indications that at least the lowest 360 m may be assignable to the Early Berriasian (Crame *et al.* 1993).

Derivation of name. Latin ‘*complanata*’, flattened; referring to the non-inflated form of this species.

Diagnosis. A small *Manticula* which does not exhibit any grossly over-inflated valves.

Description. A small–medium sized, elongate–rounded and almost smooth bivalve which tapers dorsally into a finely pointed umbo and expands ventrally to become well rounded; a number of specimens give a superficial impression of bilateral symmetry. This species is equivalve, or very nearly so (see possible minor differences, below), with no statistically significant differences between the mean lengths and widths of the best preserved left and right valves (Student’s *t*-test, $P < 0.001$).

Measurements taken on some 60 specimens indicate a mean length (L) of 35.73 mm (s.d. = 14.38, range = 12–64 mm), mean width (W) of 25.22 mm (s.d. = 9.37, range = 9–44 mm) and mean W/L of 0.712 (s.d. =

0·069, range = 0·48–0·83). There is a spectrum from more or less bilaterally symmetrical specimens (e.g. Pl. 1, fig. 2) to obviously obliquely elongated ones (e.g. Pl. 1, fig. 7). In the latter there are clear traces of a short, straight posterodorsal hinge, together with a variably-developed radial, posterodorsal furrow. It is just possible that this feature is more deeply impressed in left than right valves (Pl. 1, figs 7–10). In a typical specimen, the outline in the posterodorsal region is very slightly more angular than in the corresponding anterodorsal region; the ventral margin is always well rounded. The poorly defined umbonal region terminates in a sharply pointed beak. This feature rises just above the hingeline and varies from slightly prosogyrous to slightly opisthogyrous (Pl. 1, figs 1–10).

Both left and right valves are weakly inflated, with the maximum degree of inflation occurring in the umbonal and central regions of the valve. In specimens preserved in fine- to medium-grained sandstone, the principal ornament pattern comprises very fine concentric growth lines with superimposed radial growth threads. The latter can be traced from the umbo to the ventral margin, where they may become somewhat erratic in their course (e.g. Pl. 1, figs 5, 9). Some specimens preserved in mudstone reveal slightly coarser concentric ornament, which may be described as wrinkles. They also show, especially in the central regions of the valve, more pronounced radial ornament (Pl. 1, figs 1–3).

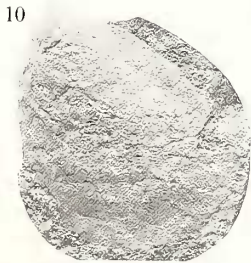
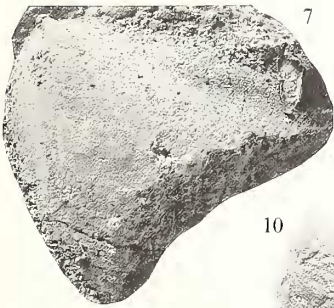
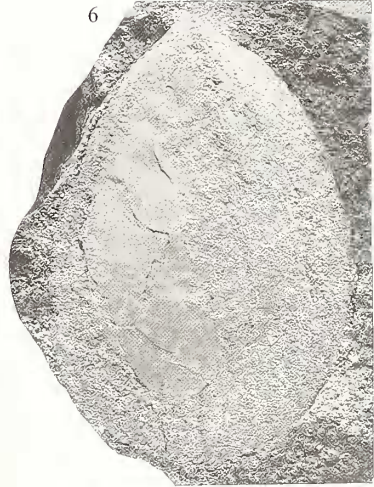
A few specimens exhibit a very clearly delimited larval shell (or prodissoconch). On P. 2201. 16 (Pl. 2, fig. 1), this takes the form of a smooth, inflated, cap-like structure bordered by an annular sulcus. In its longest dimension it measures approximately 430 μ m and towards the outer borders there are traces of a shallow depression which may mark the separation of Prodissococonch I from Prodissococonch II. In any event, it would appear that the former of these two subdivisions must have been comparatively large and this may be taken as evidence of nonplanktotrophic or even brooded larval development (Jablonski and Lutz 1980). The first 1–2 mm growth of the dissoconch proper is characterized by acute, regularly spaced, radial ribs which are crossed by faint concentric riblets (e.g. Pl. 2, fig. 1). This initial cancellate pattern is stronger than anything seen on the adult shell.

Details of the hingeline and immediately adjacent areas are particularly well preserved on three small, juvenile specimens: the internal moulds of two left valves (P. 2201. 16, P. 2233. 5; Pl. 2, figs 1–2) and the external mould of a right (P. 241. 8). All three specimens show the hinge to be a comparatively broad, complex structure whose principal features are picked out by very fine, regular growth lines. In particular, directly beneath the beak (marked by the prodissococonch) these lines pick out a prominent ridge-like fold which is broadly analogous to a tooth. In specimen P. 2201. 16 (Pl. 2, fig. 1) this ridge can be seen to slant obliquely forwards and span the whole width of the hinge area. It falls away steeply on both flanks from a comparatively sharp crest, and indications that it is hollow in the centre are confirmed by examination of P. 2233. 5 (Pl. 2, fig. 2). Anterior to the tooth-like ridge, in both left and right valves, the hinge appears to be simple, straight and marked by sub-parallel growth lines (Pl. 2, figs 1–2). However, immediately in front of the 'tooth' in both specimens, P. 241. 8 and P. 2201. 16 (Pl. 2, fig. 1), there are traces of a shallow, transverse depression which may mark the line of a narrow byssal notch.

Immediately posterior to the tooth-like ridge there are traces of a deeply impressed ligament pit. This feature is clearest in specimen P. 2201. 16 (Pl. 2, fig. 1), where it has an oblique, triangular outline and can be seen to be firmly recessed into the space directly beneath the umbo. The floor of the pit is covered by fine, sub-horizontal growth lines. In specimen P. 2233. 5 the form of the ligament pit is less obvious (Pl. 2, fig. 2), but in P. 241. 8 it is again obliquely triangular. In all three specimens the posterior segment of the hinge seems to be composed of an irregular set of elongate grooves and ridges. These features are perhaps clearest on specimen P. 2233. 5 (Pl. 2, fig. 2).

EXPLANATION OF PLATE 1

Figs 1–10. *Manticula complanata* sp. nov.; Berriasian; Byers Group; Livingston Island, Antarctica. 1, paratype, P. 1667. 6; internal mould of a probable right valve. 2, paratype, P. 1667. 20; internal mould of a right valve. 3, paratype, P. 1667. 12; internal mould of a right valve. 4, paratype, P. 2203. 1; internal mould of a left valve. 5, holotype, P. 241. 9; internal mould of a left valve. 6, paratype, P. 2153. 80; internal mould of a probable right valve. 7, paratype, P. 1668. 3; internal mould of an incomplete left valve. 8, paratype, P. 1668. 4; internal mould of an incomplete right valve. 9, paratype, P. 241. 8; internal mould of an incomplete probable right valve. 10, paratype, P. 2233. 17; internal mould of a left valve. Specimens 1–3 are preserved in mudstone, and 4–10 in fine sandstone. All are $\times 1$.





TEXT-FIG. 2. Scanning electron micrograph of crossed-foliated shell structure in the hinge region of a probable right valve of *Manticula complanata* sp. nov. (P. 2233.6); $\times 1560$.

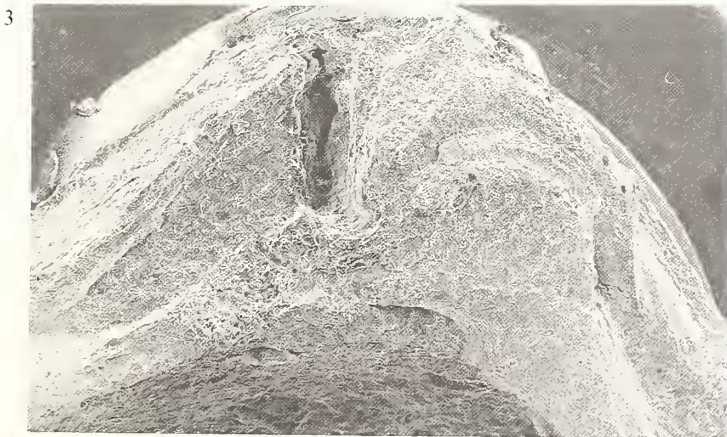
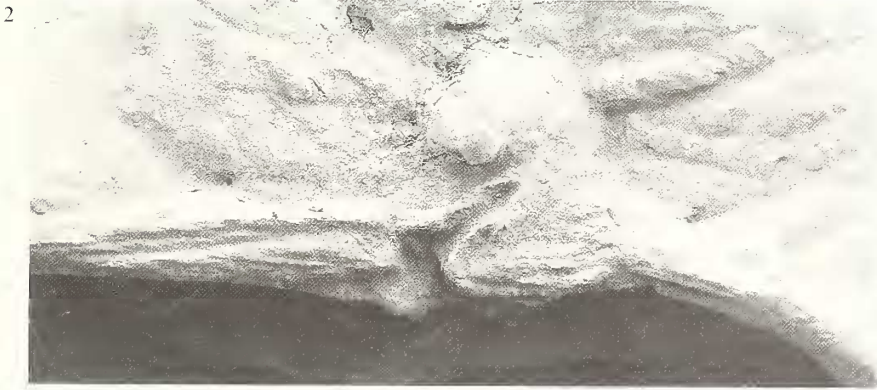
Only thin (< 1 mm) remnants of shell material are preserved on any specimen. As far as can be determined, these are nearly always calcitic in nature and crossed-foliated in structure (Text-fig. 2). This type of shell material has been detected in several parts of both left and right valves (including both hinge regions). Although nearly always showing signs of alteration, it can be seen to comprise at least two orders of obliquely orientated lamellae which intersect at a low angle (Text-fig. 2). Occasionally, this foliated layer passes into a fine grained homogeneous zone which may represent an altered inner aragonitic layer. It is noticeable too, how a few mudstone moulds have an iridescent, nacreous sheen. A band of prismatic shell material in the central region of specimen P. 2233.6 is taken to represent a myostracal shell layer.

Discussion. The material described here bears a striking resemblance to the smallest specimens of *Manticula problematica* (Zittel), the type species of the genus from the Late Triassic (Carnian–Norian) of New Zealand and New Caledonia (e.g. Pl. 3, figs 1–4). There is a considerable degree of overlap in both overall valve outlines and the form of the narrow, pointed beaks; in addition, at least some small specimens of *M. problematica* possess a radial, posterodorsal depression (e.g. Wilckens 1927, pl. 2, fig. 6). However, some of the prolific New Zealand material exhibits rather straighter anterior margins and there is an impression of a slightly more prominent umbonal region than in the Antarctic species (Pl. 3, figs 1–4).

The most obvious difference between *Manticula complanata* sp. nov. and *M. problematica* is in their respective maximum sizes. Whereas the former reaches no more than 64 mm in length, the latter can be in excess of 110 mm. The larger New Zealand and New Caledonian forms are obviously more inflated, with some specimens exhibiting a dramatic expansion of the ventral margins to produce a bizarre, gibbous shape (Pl. 3, figs 5–6). Such specimens were the basis of Trechmann's (1917) new species, *Mytilus mirabilis* (= *Mytilus trechmanni* Waterhouse, 1960), but it is now apparent that there is every gradation between the most flattened forms of *Manticula problematica* and the grossly inflated *M. trechmanni*; the two species have thus been synonymized (Waterhouse 1960). Although it has been claimed that the gibbous form is a feature of the right

EXPLANATION OF PLATE 2

Figs 1–3. Scanning electron micrographs of the hinge region of *Manticula*. 1, P. 2201.16; beak and central hinge region of a juvenile left valve of *M. complanata* sp. nov.; further details of the slanting, tooth-like ridge, triangular ligament pit and cap-like prodissoconch are given in the text; $\times 60$. 2, P. 2233.5; beak and central hinge region of a juvenile left valve of *M. complanata* sp. nov.; slanting, tooth-like ridge and ligament pit partially eroded; $\times 20$. 3, TM 7672; locality GS14977; rubber peel from an internal mould of a left valve of *M. problematica* (Zittel); behind a blunt, rounded anterior lobe (right hand side) is a deeply impressed subcentral resilifer; further details given in the text; $\times 12$.



valve only (Waterhouse 1960), it would seem that in a number of instances it is genuinely difficult to distinguish left from right (e.g. see Avias 1953, pl. 24, figs 1–3). It is unclear whether two gibbous valves would have been in juxtaposition, or whether one was always paired with a flatter, lid-like valve.

It is apparent that the largest New Zealand specimens have greatly thickened shells, with thicknesses of 6–7 mm being recorded in the hinge region (Waterhouse 1960). Much of this is due to very prominent outer calcitic layers in which irregular to branching crossed-foliated structures predominate (Waterhouse 1960; Carter 1990*a, b*). The innermost, aragonitic layers apparently have a crossed-lamellar structure.

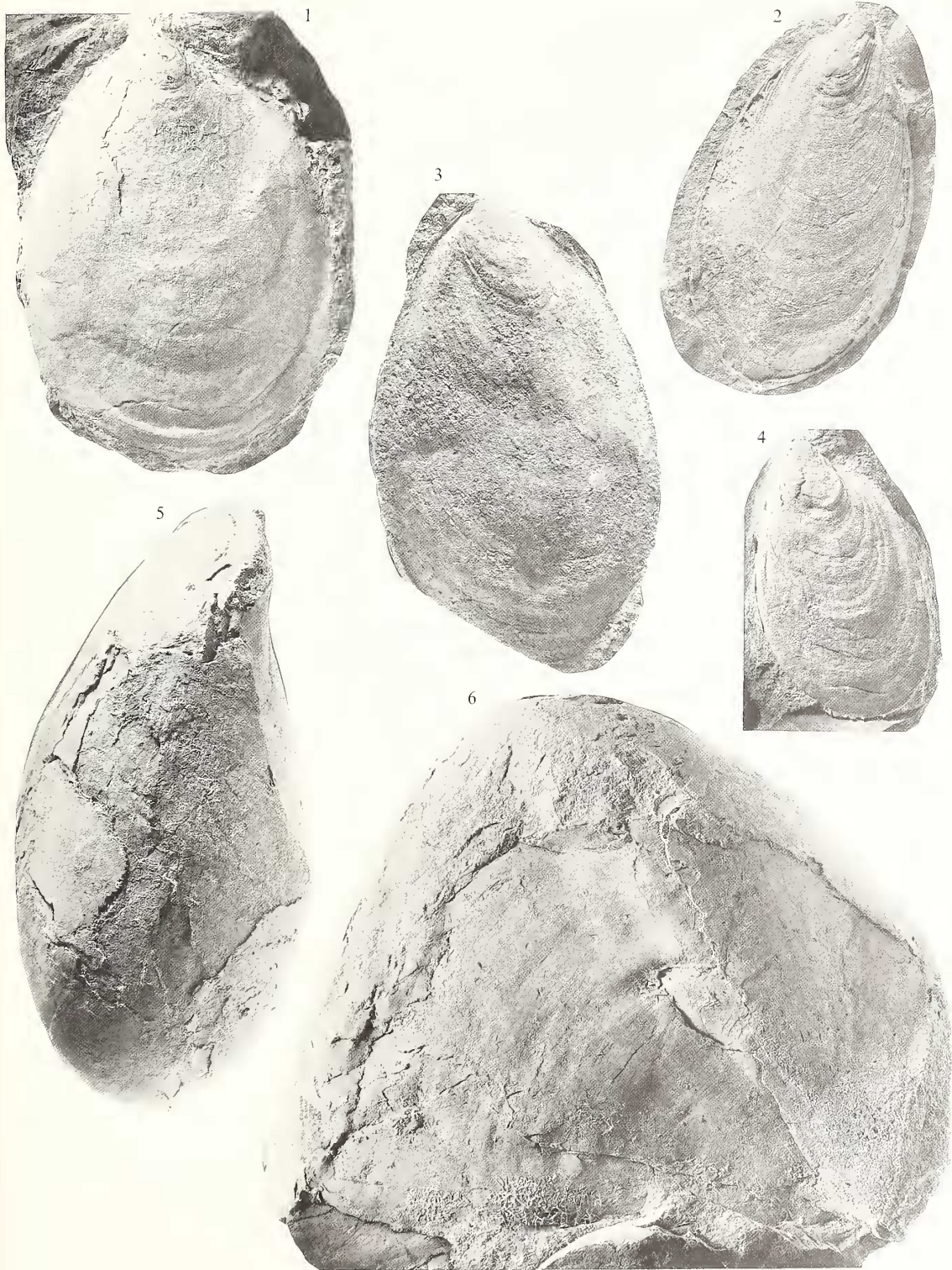
Despite the large number of specimens that have been collected, our knowledge of the hinge area of *M. problematica* is still incomplete. There has been a general recognition that it is comparatively broad, striated by growth lines and edentulous, but only very rarely is it preserved in its entirety (Trechmann 1917; Wilckens 1927; Marwick 1953; Waterhouse 1960, 1979). In the specimens described by Waterhouse (1960), the ligament appears to have been mounted in the right valve on a small striated plate (or septum) which overlies an umbonal cavity. This plate has a triangular form and terminates abruptly anteriorly against the thickened margin of the shell (Waterhouse 1960, pl. 20, fig. 3). In the adult left valve, there are again impressions of a comparatively small, triangular ligament area, but the specimen illustrated by Waterhouse (1960, pl. 21, fig. 4) is partially distorted. Examination of further adult specimens of *M. problematica* from locality GS14977, Eighty-Eight Valley, Nelson, New Zealand, has confirmed that the crucial central region is rarely preserved in its entirety. This is probably because of its location on a septal plate which overlies a deep umbonal cavity. Nevertheless, several specimens indicate that there has been a considerable degree of thickening in this region in both left and right valves, with distinct traces of an anterior blunt, rounded, tooth-like fold. This is most apparent in specimen TM 7672, where it is situated in front of what is taken to be a deeply impressed elongate-triangular resilifer (Pl. 2, fig. 3).

There is now some evidence to suggest that, as the hinge region of *Manticula* develops, it becomes considerably thickened and simplified in form. Certainly in the left valve, it would appear that the anterior, narrow, tooth-like ridge may have become transformed into a much blunter, lobe-like feature (Pl. 2, figs 1–3). In addition, it may also be that a sub-central, oblique, triangular resilifer is a consistent feature of the genus. Quite how the two valves would have articulated is not known for certain; were the tooth-like ridges in close juxtaposition or was one set slightly in front of the other? Whereas some specimens might suggest the presence of a resting groove (or socket) directly in front of the tooth, others show no sign of it. As suggested previously by Trechmann (1917, p. 201), it is more likely that this was the position of a shallow byssal sinus (e.g. Pl. 2, figs 1–2).

The presence of a thickened, striated hinge region bearing a prominent, tooth-like fold undoubtedly links this material to the Pergamidiidae; no other pteriomorph bivalve family possesses such an arrangement (see further discussion, below). Within this taxon there is a particularly close resemblance externally to small forms of *Manticula*, and this would appear to be the best genus for the new Antarctic specimens. Of course, it could be argued that lack of large, gibbous forms in the Antarctic collections, together with uncertainty about the nature of the hinge in New Zealand specimens, casts some doubt upon this assignment. Nevertheless, it is felt that, at

EXPLANATION OF PLATE 3

Figs 1–6. *Manticula problematica* (Zittel), Carnian–Norian; Eighty-Eight Valley, Nelson, New Zealand. 1, NHM L.51985; internal mould of a probable left valve. 2, TM 7673; locality GS14977; rubber peel from an external mould of a right valve. 3, TM 7674; same locality as 2; internal mould of an indeterminate valve. 4, NHM L.41262; internal mould of a probable left valve; figured previously by Trechmann (1917, pl. 20, fig. 8). 5, NHM L.41266, holotype of *Mytilus mirabilis* Trechmann, 1917 (= *Mytilus trechmanni* Waterhouse, 1960, a subjective synonym of *Manticula problematica*; Waterhouse 1960, p. 426). 6, the same specimen as 5, viewed from the anterior; figured previously by Trechmann (1917, pl. 20, fig. 9a). All are $\times 1$.



CROME, *Manticula problematica*

the present state of our knowledge, it is better to place the Antarctic material within *Mantidula* rather than create a new genus.

RELATIONSHIPS AND DISTRIBUTION OF *MANTIDULA*

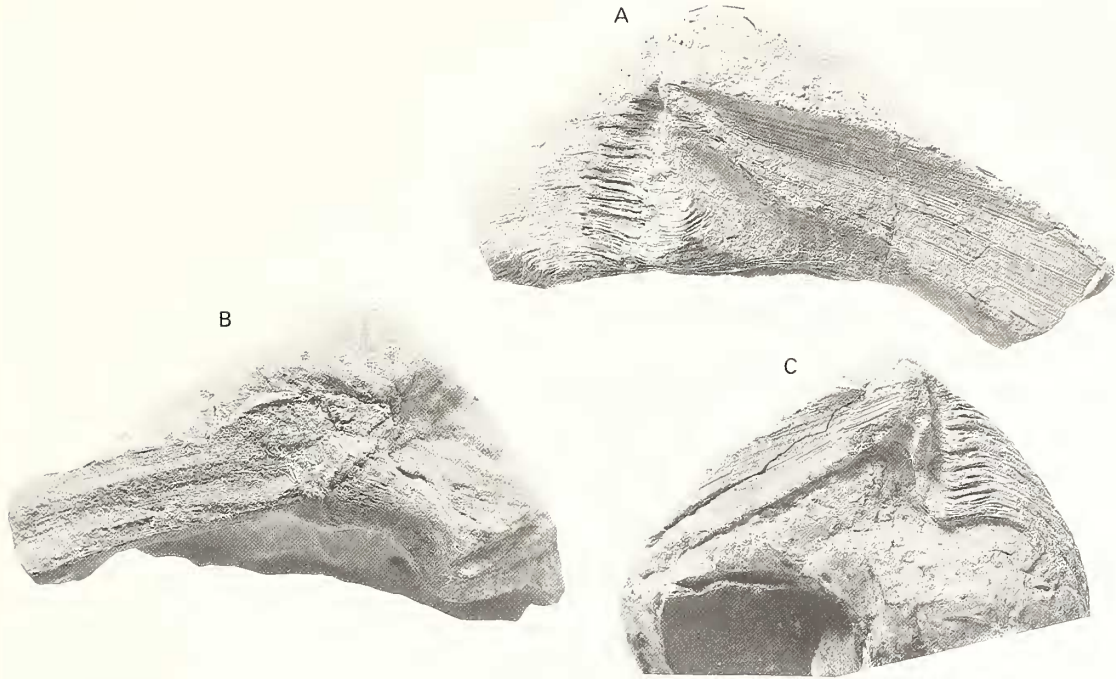
In early studies of the genus, opinion varied as to whether *Mantidula* should be classified within the Mytilidae Rafinesque, 1815 or the Myalinidae Frech, 1891 (Trechmann 1917; Wilckens 1927; Avias 1953; Marwick 1953). Even when more material became available for study, Waterhouse (1960) was unable to differentiate with certainty between these two categories. In the *Treatise on invertebrate paleontology*, Cox (1969) placed *Mantidula* within the Pergamidiidae, a new family situated close to the Inoceramidae, within the superfamily Pteriacea Gray, 1847. This taxon comprised four genera with a combined stratigraphical range of Upper Triassic–Lower Jurassic. They are distinguished collectively by their weakly ornamented mytiliform and sub-mytiliform shapes, although it should be emphasized that the genus *Pergamidia* Bittner, 1891 has an atypical anterior ear and some unusual antero-ventral radial ornament (Cox 1969, fig. C44). The sole Lower Jurassic representative, *Semuridia* Melville, 1956, may be distinguishable by its nacreous inner shell layers (Carter 1990a), but its anatomy is still far from being fully understood.

The two most prolific pergamidiid genera, *Mantidula* and *Krumbeckiella* Ichikawa, 1958, are characterized by thickened, striated hinge regions which bear a distinctive saddle-shaped fold beneath the beak; this is perhaps best described as a tooth (or tooth-like ridge) in juvenile specimens of *Mantidula* and an 'ear' in *Krumbeckiella* (Pl. 2, figs 1–3; Text-fig. 3C). The ligament area in both genera is essentially opisthodetic, and contains a variably developed central resilifer.

Krumbeckiella is a similar-sized genus to *Mantidula* but can be distinguished externally by its more oblique outline and protruding anterior margin (e.g. Krumbeck 1924, pl. 195, figs 6, 8, 9a); in some extreme forms the outline is almost quadrate (e.g. Krumbeck 1924, pl. 196, figs 6a, 7a). From the inside, the anterior ear can be seen to overhang an anterior depression which takes the form of a small lunule in the right valve and a byssal slit in the left (Text-fig. 3C; Krumbeck 1924, pl. 195, figs 3b, 9b). Such is the deeply impressed nature of the latter feature in some specimens that the anterior ear is clearly visible from the outside (Krumbeck 1924, pl. 195, figs 12b, c).

One of the most closely related genera to both *Mantidula* and *Krumbeckiella* may be the Early Permian austral taxon *Eurydesma* Morris, 1845. Although considerably larger and thicker-shelled (some forms reach 160 mm in length), it is characterized by a striated hinge region which bears a prominent saddle-shaped fold (or ear; see Waterhouse and Gupta 1982) directly beneath the beak (Text-fig. 3A–B). Such folds are particularly evident in juveniles and smaller species such as *Eurydesma playfordi* Dickins and *E. cordata* Morris (Dickins 1957; Runnegar 1970). In large, adult specimens of *Eurydesma*, the opisthodetic ligament is mounted on a broad platform which occasionally bears traces of a shallow resilifer (e.g. Waterhouse 1980, fig. 6); otherwise, the ligament surface exhibits subparallel growth striae (Text-fig. 3A–B). The shell structure of *Eurydesma* is still not known for certain, but it would appear that the greatly thickened outer calcitic layers have a predominantly foliated structure, with some minor homogeneous and simple prismatic material (Runnegar 1970, 1979; Carter 1990a, b). In this respect there would appear to be a very close correspondence with *Mantidula*; a right valve of *M. problematica* examined by Carter (1990a) was found to be almost identical in shell structure to *Eurydesma playfordi*.

There is probably a direct line of descent from *Eurydesma* to the genus *Glendella* Runnegar, 1970, which has so far only been described from the early Middle Permian of Queensland, Australia (Runnegar 1970). Also globular in shape and almost smooth, *Glendella* possesses a comparatively broad hinge along which an acute fold in the growth lines picks out a structure analogous to the *Eurydesma* 'ear'. However, it is apparent that *Glendella* is strongly inequivalve, with a large, inflated left valve and smaller, flatter right valve. There are some indications that the ligament area of this right valve is carried more on its dorsal surface and it also possesses a narrow, slit-like byssal notch (Runnegar 1970, pl. 18, fig. 4). Although the correspondence is not exact, there are a number of



TEXT-FIG. 3. The hinge region of *Eurydesma* and *Krumbeckiella*. A–B, *Eurydesma cordata* Morris. A, NHM PL4043; right valve showing prominent, subcentral tooth slanting obliquely forwards; the crest of the tooth bears a shallow depression which marks the point of articulation with the left valve tooth; prominent byssal notch lies immediately in front of the tooth; broad ligament area with fine, subparallel growth striae lies behind it; $\times 1.5$. B, NHM 8-12-5; left valve showing broad, subcentral tooth with narrow crest; $\times 1.5$. C, *Krumbeckiella subtimorensis* (Krumbeck). Mineralogisch-Geologisch Museum, Delft, No. 12933; left valve, a subcentral, ridge-like fold forms the basis of an anterior 'ear' (N.B. the crest is slightly eroded in this specimen); immediately in front of the 'ear' there is a narrow but deep byssal notch and immediately behind it a broad, flat ligament area bears traces of a shallowly impressed, triangular pit; the obliquely sloping anterior margin of this pit is clearly seen; $\times 1.5$; figured previously by Krumbeck (1924, pl. 17, fig. 9b).

points of similarity between *Glendella* and *Manticula*. These include: their inequivalve nature (at least in certain adult forms), possession of a thick crossed-foliated outer shell layer, and similar hinge regions (Runnegar 1977; Waterhouse 1980). Because of features such as its globular, strongly inequivalve form and its primitive ear and notch in the right valve, it has also been suggested that *Glendella* may be the earliest representative of the widespread monotoidean family, Buchiidae Cox, 1953 (hitherto Triassic–Cretaceous; Waterhouse 1980; Waterhouse and Gupta 1982).

It is accepted generally now that *Eurydesma* should be classified within its own family, the Eurydesmidae Reed, 1932 (e.g. Runnegar 1979). Because of overall similarities to Late Palaeozoic taxa such as *Posidoniella* Koninck (Ambonychiidae) and *Atomodesma* Beyrich (Inoceramidae), most authorities have in turn assigned the Eurydesmidae to the superfamily Ambonychioidea Miller, 1877 (Kaufmann and Runnegar 1975; Dickins 1983); this is probably the best category for the Pergamidiidae too (Carter 1990a). Nevertheless, the presence of a distinct right valve byssal notch suggests at least some pectinoid affinities for *Eurydesma* (Runnegar 1970; Carter 1990a), and whether *Glendella* is best assigned to the Eurydesmidae or Buchiidae is, perhaps, still a moot point (Runnegar 1979; Waterhouse 1980). Possible phylogenetic links between the pteroid superfamily Ambonychioidea and the pectinoid Monotoidea need to be investigated further. Waterhouse and

Gupta (1982), for example, have gone so far as to suggest that the Eurydesmidae, Pergamidiidae and Buchiidae may collectively be distinct enough to comprise a separate superfamily (the Eurydesmatoidea Reed, 1932).

Eurydesma is a consistent component of Permian cool-temperate marine invertebrate assemblages throughout Gondwana. It has been recorded from both eastern and Western Australia, India (various localities), South Africa and Argentina (Runnegar 1979, fig. 2). As stated previously, *Glendella* is known only from the Middle Permian of eastern Australia and *Manticula* occurs in the Late Triassic (Carnian–Norian) of both New Zealand and New Caledonia. *Krumbeckiella* is prolific in the Late Triassic (Norian) of Timor in a palaeoenvironmental setting which is judged to have been close to the southern margins of the Tethyan Ocean (Audley-Charles 1988). At this locality it co-occurred with *Pergamidia*, which is known from Turkey, and possibly other Tethyan Triassic localities too (Cox 1969).

Thus it is possible to conclude that the group of taxa represented by *Eurydesma*, *Glendella*, *Manticula* and *Krumbeckiella* is essentially a southern one with high-latitude, cool-temperate origins in the Early Permian. The group may well have spread subsequently so that by the Late Triassic it came to occupy marginal-Tethyan environments. Indeed, if *Pergamidia* is a valid further member of the group, it may well have disseminated through the Tethyan realm proper. Thereafter, however, the story would appear to be one of dramatic range retraction, for there may well be no true Jurassic representatives of either the Eurydesmidae or Pergamidiidae. The sole further stratigraphical record is now established for *Manticula* in the Early Cretaceous of Antarctica. Such an occurrence may well indicate that this genus became a relict in a high-latitude refugium. It may also be that it can be regarded as a Late Triassic (Carnian–Norian)–Early Cretaceous (Berriasian) Lazarus Taxon (Jablonski 1986), with no known Jurassic records. However, it is apparent that *Manticula* is still known from comparatively few stratigraphical levels in New Zealand and New Caledonia, and application of 95 per cent. confidence intervals to its Triassic range (*sensu* Marshall 1990) could see an extension into the Cretaceous. Precise stratigraphical occurrences of *Manticula* are currently being reinvestigated.

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J. A. CRAME
British Antarctic Survey (NERC)
High Cross
Madingley Road
Cambridge CB3 0ET, UK